Variation in the species richness of parasitoid wasps (Ichneumonidae: Pimplinae and Rhyssinae) across sites on different continents

ISRR AEL C. GÓMEZ, ILARI E. SÄÄKSJÄRVI, PETER J. MAYHEW, MARC POLLET, CARMEN REY DEL CASTILLO, JOSE-LUIS NIEVES-ALDREY, GAVIN R. BROAD, HEIKKI ROININEN and HANNA TUOMISTO

Abstract. 1. The old idea that parasitoid wasps (Ichneumonidae) show an inverse latitudinal diversity gradient has recently been challenged, but how ichneumonid species richness varies across the globe is still not well understood. We carried out field inventories in 21 sites on three continents to clarify this question, focusing on the subfamilies Pimplinae and Rhyssinae. Our total sampling effort was 628 Malaise trap months and the total catch exceeded 65 000 individuals. Our main focus was in two intensively inventoried areas in Amazonia, together yielding 257 Malaise trap months and 26 390 ichneumonid individuals.

2. To expand the scope and assess global species diversity patterns of the Pimplinae and Rhyssinae, we compiled published species lists from a total of 97 study localities around the world. The highest observed species richness in any locality, 105 species, was found in one of our field sites in Peruvian Amazonia. None of the other localities reported more than 70 species, even the ones with a sampling effort comparable to ours.

3. Despite the local thoroughness of our field inventories in Amazonia, data analyses indicated that a substantial proportion of the parasitoid wasp species occurring in each site remained unobserved.

4. The highest local species richness values were reported from the tropics. Nevertheless parasitoid wasps are still too sparsely sampled to draw solid conclusions about whether or not their species richness follows a particular latitudinal trend, and if so, where their richness peaks.

Key words. Amazonia, biodiversity, biogeography, latitudinal gradient, Peru, Pimplinae, rain forest, Rhyssinae.

Introduction

The parasitoid wasp family Ichneumonidae is the most species-rich hymenopteran family, and it is among the most diverse animal groups on Earth. Interestingly, it has been
suggested that the Ichneumonidae is less species-rich in tropical regions than at higher latitudes, i.e. that the family presents an inverse latitudinal diversity gradient (e.g. Owen & Owen, 1974; Timms et al., 2015). Over the years, various hypotheses have been proposed to explain why ichneumonids are relatively species-poor in the tropics (Santos & Quicke, 2011). The high number of newly described taxa in recent taxonomic publications shows that tropical ichneumonids are still incompletely known (e.g. Aguiar & Ramos, 2011; Broad et al., 2011; Santos & Aguiar, 2013). Therefore, further large-scale and long-term studies are needed, especially in the tropics, to improve our knowledge about global ichneumonid diversity patterns.

Amazonia is the largest rainforest area in the world, but also one of the least known in terms of its insect fauna. Although western Amazonia is famous for its high diversity in several animal and plant groups (Gentry, 1988, 1992; Robbins et al., 1996; Robbins & Opler, 1997; Patterson et al., 2006), some early authors proposed that ichneumonid diversity is low in Amazonia (Porter, 1978). These studies were based on small data sets, and the situation has changed in the 2000s, as new studies on Amazonian ichneumonid diversity have challenged the old paradigm (Sääksjärvi et al., 2004; Veijalainen et al., 2013; Gómez et al., 2015).

In this study, we compare observations of local species richness of pimplines and rhyssines across latitudes on the basis of field sampling we carried out in 21 sites on three continents. The two most intensively studied areas were in Peruvian Amazonia, where the sampled localities were selected so as to span different forest types (Sääksjärvi et al., 2004; Gómez et al., 2014, 2015). Most sampling was done with Malaise traps, but in the two Peruvian areas, we also used other sampling methods for comparison.

The main aims of this study are (i) to document how species accumulation of pimpline and rhyssine wasps relates to sampling effort in our two well-sampled Amazonian sites, and (ii) to assess global patterns in pimpline and rhyssine species richness using data from both our own inventories and from publications of other researchers.

Material and methods

Study organisms

The parasitoid wasp family Ichneumonidae currently includes about 40 subfamilies, 1600 genera and 24 000 described species (Aguiar et al., 2013), making it the most species-rich family within Hymenoptera. Here we focus on two of the most extensively studied subfamilies in the Neotropical region, Pimplinae and Rhyssinae (e.g. Porter, 1978; Gauld, 1991; Gauld et al., 1998, 2002; Sääksjärvi et al., 2004; Gómez et al., 2009, 2014, 2015; Gómez & Yabar, 2015).

The subfamily Pimplinae is a relatively large, cosmopolitan group with about 78 genera (Pham, 2013) and more than 1500 described species worldwide (Yu et al., 2012). This is the most biologically diverse of all ichneumonid subfamilies and it is associated with a wide range of hosts (Gauld, 1991). The species are mainly idiobiont ectoparasitoids of immature stages of holometabolan insects or idiobiont endoparasitoids of lepidopteran or hymenopteron pupae. Nevertheless the species of the Polysphincta genus-group are koinobiont ectoparasitoids of immature and mature spiders (Gauld & Dubois, 2006).

The subfamily Rhyssinae is a relatively small, cosmopolitan group with eight genera worldwide and more than 250 described species (Gómez et al., 2015). According to Kamath and Gupta (1972), the species-richness of Rhyssinae is highest in the lowland rainforests of South-East Asia. In the Neotropical region the species are believed, on the basis of the known biology of a few Old World species, to be idiobiont ecytoparasitoids of immature stages of endopterygote insects boring in wood (Gauld, 1991).

Study sites

We carried out intensive long-term sampling in two sites in Peruvian Amazonia, Allpahuayo-Mishana in the north and Los Amigos in the south. In addition, we sampled 19 sites outside Amazonia. The distribution of these sites is shown in Fig. 1. Elevation, geographical coordinates and sampling effort of each locality are given in Supplementary materials (Table S1).

Allpahuayo-Mishana National Reserve (3°57’58”S, 73°25’26”W) is located in northern Peruvian Amazonia in the department of Loreto. The climate is tropical, with mean annual precipitation of about 3000 mm and mean annual temperature of 26 °C (Marengo, 1998). Elevation is between 100 and 180 m above sea level and the prevailing vegetation is moist tropical forest according to the Holdridge (1967) classification. The environmental conditions have been described in Kalliola and Flores-Paitan (1998). Our ichneumonid sampling was carried out in non-inundated areas (terra firme), where the terrain is divided among three main soil types. Flat low-lying areas often have soils derived from the marine Pebas formation of Miocene age. These soils are clayey in texture, relatively rich in nutrients, and mostly brownish-grey in colour (Kalliola & Flores-Paitan, 1998). The tops of the plateau-like hills often have white sand soils, which are nutrient-poor and white or grey in colour. Loamy soils are probably derived from old river terraces (Kalliola & Flores-Paitan, 1998). The forests growing on the clayey to loamy soils have a classical rain forest physiognomy with large trees and different canopy layers, whereas the white sand forests have slenderer trees and a less complex canopy structure (Anderson, 1981; Tuomisto & Ruokolainen, 1994).

Los Amigos Conservation Concession (12°33’34” S, 70°04’05” W) is located in the southern Peruvian Amazonia in the department of Madre de Dios close to the Andean-Amazonian interface. Mean annual precipitation is about 2770 mm and annual mean temperature 23 °C.
with monthly mean temperatures varying 20–26 °C (Gómez et al., 2009). This is somewhat drier, cooler and more seasonal than in Allpahuayo-Mishana. Elevation varies between 230 and 270 m above sea level and the vegetation is moist tropical forest according to the Holdridge (1967) classification. For description of the environmental conditions, see Wilson and Sandoval (1996). The Los Amigos watershed comprises sediments dated from the Neogene and Quaternary that have been deposited during the last 20 million years (Pino, 2007). Due to the proximity of the Andes, the soils are a mosaic of clayey, sandy, silty and gravelly materials, but extremely nutrient-poor soils such as white sands have not been reported for the area. Our ichneumonid sampling covered both non-inundated and seasonally inundated forests. In general, terra firme soils are sandier, more acidic and poorer in nutrients than those located in the floodplains (Hovikoski et al., 2005).

Seven of our other 19 sampling localities are located in temperate South America between the regions of Maule (35°S) and Los Lagos (42°S) in Central Chile. One sampling locality is in Central America on Coiba island off the Pacific coast of Panama (7°N). This is a national park and the vegetation is moist tropical forest according to Holdridge’s classification.

Eight sampling localities were established in the temperate region of Spain, between 38°N and 42°N; for details see Nieves-Aldrey (1995); Nieves-Aldrey et al. (2003).

Three localities are situated in the Canary Islands in Isla de la Palma (28°N) and were mostly dominated by forests of the endemic Canarian pine (Pinus canariensis Chr. Sm. ex DC; for survey details see Domingo Quero et al., 2003). One sampling locality is in central Africa, the Kibale National Park in Uganda.

**Sampling methods**

Our primary sampling method consisted of long-term Malaise trapping. A Malaise trap is an open tent-like structure widely used in entomological studies, and ichneumonid surveys in particular, because it is efficient in collecting insects that are strong flyers (Nieves-Aldrey & Rey del Castillo, 1991; Sääksjärvi et al., 2004; Mayhew et al., 2009). Thanks to the popularity of Malaise traps, it was possible to find comparable data from earlier parasitoid studies, as the sampling effort can be conveniently expressed in terms of Malaise trap months (MTM). One MTM corresponds to one trap collecting in the field for a period of 1 month (or a combination of more traps that cumulatively operate for 1 month).

In the Peruvian Allpahuayo-Mishana, we combined data from three separate field campaigns. The first one ran from August 1998 to January 1999 with 12 traps and had a total sampling effort of 41 MTM. The second ran from January 2000 to January 2001 with 15 traps and had a total sampling effort of 144 MTM. Both of these campaigns have been described by Sääksjärvi et al. (2004). The last campaign was conducted by 14 Malaise traps, four of which were active in April-December 2011 and ten in October-December 2011. The total sampling effort of these traps was 45 MTM, and details have been described by Gómez et al. (2015).

In Los Amigos, nine Malaise traps were in operation in May–July 2008 with a total sampling effort of 27 MTM. The total sampling effort in Allpahuayo-Mishana and Los Amigos combined was 257 MTM. To our knowledge, this is the most extensive sampling of ichneumonids in Amazonia.

To find out if Malaise trapping might be systematically biased and miss some species entirely, we applied four additional sampling methods in Allpahuayo-Mishana and one in Los Amigos (Table 1) (i) Yellow pan traps (Moericke traps). During 23 weeks, a total of 100 traps were set out in Allpahuayo-Mishana for a period of 24 h every week. In each weekly sampling, the traps were spread across the different forest types. (ii) Hand netting with a standard entomological net. This was done weekly for 13 weeks in Los Amigos and for 23 weeks in Allpahuayo-Mishana. Each netting session consisted of 4 h of random
sweeping in the vegetation of different forest types. (iii) Larval rearing. A total of 3298 lepidopteran larvae were collected in the forests of Allpahuayo-Mishana and reared individually in 1-litre plastic jars. (iv) Pupal rearing. A total of 113 lepidopteran pupae were collected in the forests of Allpahuayo-Mishana and reared individually in 1-litre plastic jars.

The number of localities and sampling effort outside Amazonia is as follows: seven in Central Chile (45.4 MTM), one in Panama (1.4 MTM), seven in Spain (57.4 MTM), three on the Canary Islands (4.8 MTM) and one in Uganda (252 MTM). Samples from all localities were prepared and identified in the Zoological Museum of the University of Turku (ZMUT) and the National Museum of Natural Sciences, Madrid (CSIC). Voucher specimens will be deposited to ZMUT, CSIC, The Natural History Museum Universidad Nacional Mayor de San Marcos (Lima, Peru) and The Royal Belgian Institute of Natural Sciences. Taxonomy is based on Gauld (1991).

Global comparison of Pimplinae and Rhyssinae species-richness

To evaluate global patterns in Pimplinae and Rhyssinae species richness, we searched the literature for ichneumonid inventories that could be compared with our field data. Because the number of observed species is dependent on sampling effort, we only considered quantitative inventories that had used Malaise traps and in addition recorded the duration of sampling and/or the number of captured Pimplinae and Rhyssinae individuals. We found 76 studies fulfilling these criteria. In most cases, relevant information for our analysis was not available in the original publication but was kindly provided by the authors of the studies (see Table S1).

All the inventories were carried out in delimited sites with little altitudinal variation. In most cases, the variation within a locality was <200 m. It was important to ensure that all data points represented single localities; if some had included longer altitudinal gradients than others, drawing conclusions about latitudinal patterns in local species richness would not be appropriate. Some published inventories only included data on the subfamily Pimplinae. Because this subfamily is much more abundant and species-rich than Rhyssinae (Gauld, 1991), we used these data as well but identify them in the results.

Data analysis

Our first aim was to document species accumulation patterns as a function of sampling effort in the Peruvian sites, for which time series data were available. Each sampling interval (originally 1 or 2 weeks) from each trap was used as a separate sampling unit. Species accumulation curves were obtained in two different ways. First, the actual observed species accumulation was documented by aggregating consecutive sampling intervals from the beginning of a trap’s operation to its end. Second, sampling units were combined in a random order, within habitat types only, to observe patterns of species accumulation at the site level.

To take into account species abundance patterns, we calculated the effective number of species, also known as true diversity. This equals the reciprocal of the weighted mean of the proportional species abundances, with the species abundances themselves used as the weights and the parameter \( q \) defining which mean is used (Tuomisto, 2010). We used two different means, the geometric mean (corresponding to \( q = 1 \)) and the arithmetic mean \((q = 2)\). The former gives a diversity value that equals the exponential of the well-known Shannon index, and the latter gives a value that equals the inverse Simpson index.

We used the Chao-1 estimator to assess how many additional species could be expected at a site, given the number of species observed only once or twice with a given sampling effort. The estimated number of additional species was then compared with the corresponding sampling effort to check for any indication that species sampling was approaching completeness.

Division of the Peruvian data to subsets of different sampling efforts made it possible to compare richness values from elsewhere in the world with Peruvian data of similar sampling effort. Here we focus on the effect of sampling effort only, and do not take into account possible effects of seasonality. The effect of habitat heterogeneity was minimised by only pooling samples taken in the same forest type. This was done to ensure that the Peruvian species richness values are not inflated in relation to the other sites, for which information on possible habitat heterogeneity was not available. Species accumulation was plotted against both sampling effort in the strict sense (the length of the sampling interval in MTM) and sampling efficiency (the number of Pimplinae and Rhyssinae individuals captured). In addition, we analysed latitudinal and elevational trends in local species richness after taking into account the effect of sampling efficiency. This was done by first fitting a second-order polynomial regression of number of species against

### Table 1. Summary of the sampling methods and sampling effort in ichneumonid inventories in two Peruvian Amazonian sites.

<table>
<thead>
<tr>
<th>Method</th>
<th>Allpahuayo-Mishana</th>
<th>Los Amigos</th>
</tr>
</thead>
<tbody>
<tr>
<td>Collection year</td>
<td>1998</td>
<td>2008</td>
</tr>
<tr>
<td>Malaise sampling</td>
<td>41MTM</td>
<td>27MTM</td>
</tr>
<tr>
<td>Yellow pan trap</td>
<td>144MTM</td>
<td>45MTM</td>
</tr>
<tr>
<td>Hand netting</td>
<td>–</td>
<td>76.7 trap months</td>
</tr>
<tr>
<td>Larval rearing</td>
<td>–</td>
<td>92 h</td>
</tr>
<tr>
<td>Pupal rearing</td>
<td>–</td>
<td>52 h</td>
</tr>
<tr>
<td></td>
<td>3298</td>
<td>113</td>
</tr>
</tbody>
</table>

© 2017 The Royal Entomological Society, Insect Conservation and Diversity
number of individuals (both logarithmically transformed), and then using the residuals from this regression as the response variable in linear regression against latitude or elevation. All analyses were done in the R environment using either the ‘vegan’ package (Oksanen et al., 2013) or code written by HT.

Results

The 21 localities we sampled in different parts of the world produced a total catch of approximately 65,000 ichneumonid individuals, of which 2,698 individuals representing 293 species were Pimplinae or Rhyssinae. In Allpahuayo-Mishana, all sampling methods together yielded a total of 24,378 ichneumonid individuals representing 19 subfamilies. The subfamily Pimplinae was represented by 1,516 individuals (92 species) and the subfamily Rhyssinae by 81 individuals (13 species; Table S2). In Los Amigos, a total of 2,012 ichneumonid individuals representing 18 subfamilies were captured. The subfamily Pimplinae was represented by 106 individuals (42 species) and the subfamily Rhyssinae by 15 individuals (nine species; Table S2).

The two Peruvian sites had 16 genera of Pimplinae, 9 (56%) of which were shared, and a single shared genus of Rhyssinae (Table S2). The species compositions of the two sites were rather different: of the 128 Pimplinae and Rhyssinae species observed, 81 species (63%) were only collected in Allpahuayo-Mishana, 23 species (18%) only in Los Amigos, and only 24 species (19%) were shared between both localities. In other words, the overall similarity of the species compositions in the two sites equalled 0.19 if measured with the Jaccard index and 0.32 if measured with the Sørensen index. It is noteworthy that half of the species that were observed in Los Amigos were not observed in Allpahuayo-Mishana in spite of the massive sampling effort (230 MTM) in the latter. In both Peruvian sites, the Malaise trap proved to be the most efficient collecting technique, as all the Pimplinae and Rhyssinae species encountered in the inventory were found in Malaise traps. The other methods only yielded additional individuals of some of the species.

In the 2011 inventory in Allpahuayo-Mishana, Malaise trapping captured 1,961 ichneumonid individuals, which was 74% of the total captured with all methods together in that year (2,640 individuals). Yellow pan trapping yielded 511 ichneumonid individuals (19% of the total) and hand netting produced a catch of 142 individuals (5% of the total). Larval rearing produced 22 individuals and pupal rearing only four individuals. Given that 3,411 lepidopteran larvae and pupae were reared, this indicates that only a small proportion of them were parasitised by ichneumonids.

Overall, Cryptinae was the most abundant subfamily with 1,168 individuals (44% of the total), whereas Pimplinae with 205 individuals and Rhyssinae with 19 individuals represented smaller proportions of the total catch (5% and 0.7%, respectively). The individual Malaise traps differed greatly in how many individuals and species they captured per unit time, but there did not seem to be any systematic trend in this either among habitat types locally or between the two Peruvian sites (Fig. 2a, b). When species accumulation was related to the number of individuals captured, much more uniform trends were observed across the traps. There was only a modest tendency for species accumulation to slow down with increasing sampling efficiency (Fig. 2c).

The Chao-1 estimates indicated that even at the largest sample sizes within habitat types, many species still remained unobserved (Fig. 3). The estimated number of unseen species was only weakly related to the number of individuals already observed, although a decreasing tendency emerged when the sample size became larger than about 200 individuals. A linearly decreasing trend was found if the estimated number of unseen species was...
expressed as a percentage of the observed number of species (3B). Nevertheless, even at the largest sample sizes available to us, it was still estimated that the number of species would increase by 10-30% if more individuals were sampled.

The global sampling effort for Ichneumonidae that is both known to us and reports adequate data for comparison (Table S1) totals 3267 MTM. Costa Rica is the best-studied country with data available from 17 localities with a combined sampling effort of 1266 MTM (39% of the world total). Our Peruvian study contributed 19% of the world total (628 MTM). In general, most of the study sites were at relatively low altitudes with only 10 of the 97 localities (about 10% of total MTM) occurring above 2000 m elevation.

Our Malaise traps in Peruvian Amazonia were about as efficient in capturing Pimplinae and Rhyssinae individuals as the traps for which results have been reported in the literature: the number of individuals caught with any given number of Malaise traps months in our data was firmly within the limits reported from other sites with a similar number of Malaise trap months (Fig. 4a). In contrast, the number of species caught in the Peruvian traps was generally higher than the numbers of species reported for the same number of Malaise trap months elsewhere (Fig. 4b). This difference became even clearer when the number of species was shown against number of individuals: for any given number of individuals captured, the number of species observed was always highest in the Peruvian samples (Fig. 5a).

![Fig. 3. Estimated number (a) and percentage (b) of additional Pimplinae and Rhyssinae species expected if more individuals could have been added to samples currently available from Peruvian Amazonia. Each circle corresponds to the total catch in a number of original 1–2-week samples that were combined randomly but always within the same habitat type. A-M refers to Allpahuayo-Mishana (northern Peru), LA to Los Amigos (southern Peru). [Colour figure can be viewed at wileyonlinelibrary.com]](image)

![Fig. 4. Accumulation of Pimplinae and Rhyssinae individuals (a) and species (b) as a function of sampling effort (Malaise trap months) in Peruvian Amazonia (A-M and LA) and in other parts of the world (Literature). Symbols in grey correspond to samples that only reported Pimplinae. Open circles correspond to lowland sites (<1000 m elevation) and closed circles to montane sites (>1000 m elevation). Circle size is proportional to absolute value of latitude. For Allpahuayo-Mishana and Los Amigos (A-M and LA, respectively), each symbol corresponds to a combination of randomly chosen 1–2-week samples from the same habitat type. Some literature sites present in b are missing from a because they did not report number of individuals. [Colour figure can be viewed at wileyonlinelibrary.com]](image)
All the sites with more than 50 observed species were in the tropics, and the upper limit of local species richness clearly decreased towards the poles. Sites with very few observed species (even taking into account sampling effort) were found at all latitudes (Fig. 6). Therefore, no consistent overall gradient in species richness could be seen in relation to latitude. With elevation, the relationship was even weaker.

When some species are more abundant than others, the effective number of species (\(\text{\species diversity}\)) becomes smaller than the actually observed number of species. This effect was clearly visible in our Peruvian data (Fig. 5). Differences between the habitat types in species accumulation were small, but traps in white sand forests tended to yield fewer species for a given number of individuals than traps in the other habitats. Interestingly, the traps in secondary forests tended to have relatively high species richness, but these samples were dominated by a few species, which resulted in clearly decreasing diversity with increasing value of \(q\). The species diversity accumulation curves
also showed a distinct tendency to level off at a much earlier stage than the species-richness accumulation curve did.

The general impression from plotting observed species richness against latitude was that the highest numbers of species are found in the tropics (Fig. 6a). This impression was confirmed for the lowland sites when the effect of collecting efficiency (number of individuals) was taken into account, but no such trend was seen among the montane sites (Fig. 6b). Within the tropical sites, species richness seemed to decrease with elevation, but no trend was observed in the non-tropical sites (Fig. 6c).

**Discussion**

**Parasitoid wasp species-richness**

Allpahuayo-Mishana is currently the site with the highest known species-richness for pimpline and rhyssine wasps in the world, with 105 species. Our current estimate is that 27 of these (25.8%) represent already described species, whereas 78 species (74.2%) are new to science (Table S3).

The total sampling effort in Allpahuayo-Mishana was 240 MTM, which is high in global comparison (Table S1). The most intensively sampled locality in the world known to us is Santa Rosa in Costa Rica, where researchers have observed 40 species with a sampling effort of 576 MTM (Gaston & Gauld, 1993). Only four other sites can boast a sampling effort exceeding 100 MTM for Pimplinae and Rhyssinae, and none of these has reported more than 26 species (Table S1): Cerro Hacha in Costa Rica, Ria Lagartos in Mexico, Cabañeros in Spain and Kibale in Uganda. The two Peruvian localities show consistently higher numbers of Pimplinae and Rhyssinae species than most other sites when comparisons are made among subsamples based on an equivalent sampling effort (MTM; Fig. 4b). The difference becomes even more evident when comparisons are based on sampling efficiency (number of individuals; Fig. 5a).

Peruvian Amazonia is known to have high habitat heterogeneity (Tuomisto et al., 1995), and it has very high species-richness of trees (Gentry, 1988, 1992), butterflies (Robbins et al., 1996; Robbins & Opler, 1997) and birds (Patterson et al., 2006).

Pimplinae and Rhyssinae, and idiobiont ichneumonids in general, have already been documented to be species-rich groups in the tropics (Gauld, 1991; Sime & Brower, 1998; Quicke, 2012). These subfamilies are among the best-known groups of parasitoids in the Neotropics, but our results indicate that their species richness in Amazonia is even higher than previously reported by Sääksjärvi et al. (2004).

Recent findings have demonstrated that the subfamily composition of idiobiont and koinobiont ichneumonids is rather similar in temperate and tropical regions (Veijalainen et al., 2013). Furthermore, also high numbers of koinobiont species have been discovered recently from the tropics (Broad et al., 2011; Veijalainen et al., 2012; Khalaïm & Broad, 2013). These findings together with our results suggest that species richness of both idiobiont and koinobiont ichneumonids is still mainly undiscovered and most likely very high in the tropics.

The functional composition of the pimpline and rhyssine faunas in our Peruvian Amazonian study localities (Table S2) is rather similar to that in other tropical study localities (e.g. those mentioned by Gauld, 1991). Idiobiont parasitoids are clearly dominating, with the genus Neotheronia being especially abundant in the Neotropics.

**Latitudinal species-richness gradient**

Our results lend no support to the anomalous latitudinal species-richness gradient that was originally proposed by Owen and Owen (1974), at least for the subfamilies Pimplinae and Rhyssinae. We found a lot of variation in species richness within latitudes but variable sampling effort makes the results difficult to interpret. If anything, the observed maxima of local species richness follow the usual species-richness gradient, that is, the observed numbers of species peak in the tropics and decrease towards the poles. Owen and Owen (1974) examined samples collected in Northern Europe and in the Afrotropical region. They observed that “a quite extraordinary number of species was found once” in their samples, which suggests that the parasitoid wasp communities were only superficially sampled. Janzen and Pond (1975) and Janzen et al. (1976) agreed with the phenomenon of reverse latitudinal gradient but did not demonstrate that their sampling efforts were representative enough to support such broad generalisations. As a result, the phenomenon was popularised although it was based on data obtained from only a handful of study localities that were not even distributed along a proper latitudinal gradient.

In our northern Peruvian site, 2 years of sampling with several Malaise traps was insufficient to obtain a complete representation of the species in any one locality. Such an outcome is expected when sampling hyperdiverse organisms (Colwell & Coddington, 1994). Together with the results from all the parasitoid studies analysed here, this leads us to agree with the proposal that the main reason why low latitudes have been thought to be relatively species-poor for ichneumonids is insufficient sampling effort (e. g. Hespenheide, 1978; Morrison et al., 1979; Sime & Brower, 1998; Sääksjärvi et al., 2004; Santos & Quicke, 2011).

**Local species composition in peruvian amazonia**

The Malaise traps differed considerably in how many species they captured (Fig. 2). This was not related to habitat type in any obvious way, although in Allpahuayo-Mishana there was a weak tendency for traps in white sand forests to capture fewer species per unit time than...
traps in the other kinds of forest did (Fig. 4b). This would agree with earlier reports that white sand forests have fewer plant and animal species than other non-inundated forest types do (Anderson, 1981; Tuomisto & Ruokolainen, 1994). This, together with the less complex forest structure, may lead to this habitat type providing fewer niches for parasitoids. The relatively open canopy in white sand forests also makes them rather sunny and possibly dry, which is thought to be unfavourable for ichneumonids (Gauld, 1991). Nevertheless this cannot be the only explanation since secondary forest had higher species-richness than the other habitats. This parallels results from Brazilian Amazonia, where moth species richness in secondary forests was consistently higher than in primary forest (Barlow et al., 1998). The degree of dominance was also high in secondary forests: diversity (which takes species abundances into account) was clearly lower in secondary forests than in old-growth forests on loamy soils (Fig 5b), although there appeared to be no obvious difference in species richness (Fig 5a).

It is noteworthy that half of the Pimplinae and Rhyssinae species that were observed in Los Amigos were not found in Allpahuayo-Mishana, and <20% of the observed species were shared between the two sites. This may partly be due to undersampling, as the species accumulation curves indicate that part of the species pools remained unsampled in both areas. It is likely that there is also a real difference between their ichneumonid faunas, which could be due to at least two causes. First, the two sites are more than 1000 km apart, and there might already be biogeographical differences between their regional species pools. Second, the habitat types sampled in the two sites were different: sampling in Los Amigos was mostly in floodplain forests, whereas sampling in Allpahuayo-Mishana was in non-inundated forests. Therefore, any specialists of floodplain forests would have been missed in Allpahuayo-Mishana, although they might exist in the general area. Conversely, specialists of white sand forests could not have been observed in Los Amigos, as such forests are not known to occur in the area. Such possibilities open up interesting questions about the ecology and biogeography of ichneumonid wasps.

**Sampling effort**

There was considerable variation among individual Malaise traps in how many specimens and species they captured per unit time. Indeed, it is obvious that the precise placement of a Malaise trap may have a considerable impact on how many insects it captures. On the other hand, the number of individuals captured was a good predictor of the number of species observed (Fig. 5a). This suggests that when the interest is in comparing species-richness or diversity values among sites, it is more important to ensure comparable sampling efficiency (number of individuals captured) than comparable sampling effort (time spent sampling).

The total sampling effort in all our field localities (the red dots in Fig. 1) was 628 MTM, of which 257 MTM was focused on Peruvian Amazonia. The species accumulation curves for the different habitats showed that our sampling was nowhere near complete (Figs 3 and 4; Colwell & Coddington, 1994). This was true even for the most intensively studied habitat type, namely white-sand forest, which was sampled by 93 MTM in Allpahuayo-Mishana. Indeed, species-richness was still expected to increase by 10–30% if sampling were continued (Fig. 4). This parallels earlier results from Costa Rica, where only 32 Pimplinae and Rhyssinae species were known before the study of Gauld (1991). After extensive sampling programs this number increased to a total of 195 species (Gauld et al., 1998). Likewise, sampling conducted over a decade increased the number of Pimplinae species known from Vietnam from 39 to 122 (Pham, 2013). In both of these tropical countries, it took several years of sampling to produce a significant increase in the species richness. In Peru, a total of 128 Pimplinae and Rhyssinae species were recorded here from the two Amazonian localities, but more can be expected.

Most studies on parasitoid wasps have been carried out in the northern hemisphere. This has left the southern hemisphere poorly known, including the recognised diversity hotspots there (Orme et al., 2005). This situation may also be one reason for the fact that the known ichneumonid genera are heavily concentrated in the northern hemisphere (Quicke, 2012). In addition, most studies have focused on lowlands (Table S1), so information from mid and high altitude areas is sparse. Both of these biases in sampling need to be considered when studying the distributional patterns of ichneumonids.

Morrison et al. (1979) lamented that the sampling effort was insufficient in tropical and temperate regions to provide a clear understanding of species-richness patterns of these parasitoids, and we suggest that the situation has remained similar to the present day. Species accumulation curves from our intensively sampled Peruvian sites suggest that most of the study localities for which we have found published data (Table S1) are still too superficially sampled to allow a reliable estimation of local ichneumonid species richness to be made. Although the two Peruvian Amazonian localities seem to be the most species-rich sites in the world for the subfamilies Pimplinae and Rhyssinae, this may just be a consequence of the extensive sampling effort in them. The situation may well change when other sites become more intensively sampled. In the light of the currently available data, it is plausible that the species richness of Ichneumonidae (or at least Pimplinae and Rhyssinae) follows the usual latitudinal trend of highest local diversity in the lowland tropics.

**Acknowledgements**

The Ministry of Agriculture and the Ministry of Environment of Peru provided the collecting and export permits.
for the Peruvian samples. We appreciate the support of the Instituto de Investigaciones de la Amazonía Peruana (IIAP) for the field studies made in Allpahuayo-Mishana. The colleagues and the friends of the “Centro de Investigaciones Allpahuayo and Los Amigos (CICRA)” station helped considerably during the field work. Olavi Kurina, Carol Castillo and Tapani Hopkins helped with the preparation of the Afrotropical material. Michael Sharkey, Eric Chapman, (projects NSF DEB 9972024 and 0205982, cited as Sharkey, 2006), Rafael Menjivar, Gergely Várkonyi, Enrique Ruiz-Cancino, Claire Villemant and Santiago Bordera kindly provided data on the field inventories conducted by them. We thank A. Bennett for helpful comments on the manuscript. The study was partly funded by the Kone Foundation, Finland (a grant awarded to the project: Biodiversity and multiple trophic interactions lead by Ilari E. Sääksjärvi). Israël C. Gómez thanks the support of the following foundations: the Amazon Conservation Association (Peru), Conservation International Foundation-Peru and the Turk University Foundation. Marc Pollet is indebted to the Leopold III Fund (Belgium) for providing support for the Chilean survey. Field work in Los Queules and Huinay (Chile) was funded by research projects FONDECYT 1050745 and “Ayudas para la realización de estancias de investigación en el centro científico de la Fundación Huinay” (CSIC-Endesa), grants to J. L. Nieves-Aldrey.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: doi: 10.1111/ icad.12281:

Table S1. Species-richness of Pimplinae and Rhysiniae in 97 sites sampled with Malaise traps around the world.

Table S2. Abundance, species richness and functional type of the Pimplinae and Rhysiniae genera found in the Peruvian localities Allpahuayo-Mishana and Los Amigos.

Table S3. List of described species of Pimplinae and Rhysiniae (Hymenoptera: Ichneumonidae) found from Allpahuayo-Mishana, Peru.

References


© 2017 The Royal Entomological Society, Insect Conservation and Diversity


Pinto, D. (2007) Distribution and Habitat Preferences of Lecithidiinae in the Los Amigos Uplands, South Western Amazonia